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Experimental degradation of plant materials in Hudson river sediments

I. *Heterotrophic transformations of plant pigments*

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Abstract. We examined photopigment degradation and transformation in sediment microcosms that received different detrital source materials (planktonic, littoral, terrestrial) in the presence or absence of amphidpods (*Gammarus* sp.). Additions of realistic quantities of particulate organic matter resulted in detectable changes in pigment concentration and composition despite insignificant changes in total organic matter. The transformation of chlorophyll *a* to total phaeophorbide was significantly higher in all high quality (high nitrogen) detritus treatments containing amphipods. The highest production of phaeophorbide was in the higher quality detritus (blue-green algae, *Anabaena cylindrica*, and macrophyte, *Vallisneria americana*) when compared to red maple (*Acer rubrum*). Phaeophytin formation was not related to amphipod grazing and thus may be determined more by microbial heterotrophic processes. The degradation product of the carotenoid lutein, lutein 5,6 expoxide, was formed in all treatments. Phaeopigment composition can be used to infer differences in heterotrophic activity and will help in the interpretation of photopigment distribution in field samples.

Introduction

There are a diverse array of plant sources (terrestrial, littoral, planktonic) that enter into the food webs of estuarine and riverine ecosystems (Wetzel 1983; Valiela 1984; Peterson & Howarth 1987; Henebry & Gorden 1988). The decay and fate of these sources to the heterogeneous detritus pool is of considerable interest to understanding energy flow and production in aquatic ecosystems (Tenore et al. 1982; Valiela 1984). Characteristic plant pigments can serve as tracers of organic matter in natural systems (Gorham 1960; Daley 1973; Watts et al. 1977; Repeta &

Gagosian 1987; Bianchi & Findlay 1990). Chlorophyll and carotenoid pigments, which are found in all plants, exhibit class-specificity that can be used to trace organic matter flow in freshwater and marine ecosystems.

The degradation products of pigments, formed primarily by heterotrophic processes, are the most abundant forms of pigments found in sediments (Daley 1973; Repeta & Gagosian 1987; Furlong & Carpenter 1988). These pigment degradation products may be used to infer the availability of different source materials to consumers. For example, the three dominant tetrapyrrole derivatives of chloropigments (phaeopigments) found in marine and freshwater systems (chlorophyllide, phaeophytin, phaeophytin, phaeophorbide) are formed during bacterial, autolytic cell lysis, and metazoan grazing activities (Sanger & Gorham 1970; Jeffrey 1974; Shuman & Lorenzen 1975; Welschmeyer & Lorenzen 1985). The most abundant chloropigment derivative found in sediments is phaeophorbide, which is closely associated with metazoan grazing activity (Daley 1973; Shuman & Lorenzen 1975; Brown et al. 1981; Welschmeyer 1985; Hawkins et al. 1985; Carpenter & Bergquist 1985; Bianchi et al. 1988). Differential production of phaeophorbide during grazing activity on different plant resources should be reflective of differences in resource utilization. Therefore, high quality or preferred food materials should exhibit the most rapid accumulation of phaeophorbide.

To understand fully the temporal and spatial variability of pigment concentrations in the field, we feel it is necessary to first conduct controlled laboratory experiments to provide information on:

— the signal associated with additions of known plant material; and
— the temporal persistence of the signal.

We used laboratory microcosms containing Hudson River sediments and water to examine the heterotrophic transformation of plant pigment. We used three different source materials that represent terrestrial, littoral, and planktonic source inputs (red maple, *Acer rubrum*; water celery, *Vallisneria americana*; and the blue-green alga, *Anabaena cylindrica*) in Hudson River sediments. We also examined the effects of a macroconsumer (*Gammarus* sp.), which represents an abundant macrofaunal species in the tidal freshwater Hudson (Simpson et al. 1986). This experiment allowed us to examine how and at what rate different plant pigments are transformed by heterotrophic processes in Hudson River sediments. The results from such work should prove useful for interpretion of seasonal changes in pigment concentrations in river or lake sediments (Leavitt & Carpenter 1990).

Methods

Experimental animals, sediments, and plant materials

The experimental animals, *Gammarus* sp. (Amphipoda: Crustacea), were collected from the Mid-Hudson River near Kingston, N.Y. Sediment was collected from the same location, wet-sieved (<500 μm) and allowed to stand at room temperature before being used in the laboratory microcosms.

Acer rubrum was collected from a tributary of the Hudson River and *Vallisneria americana* from a shallow area of the Hudson just north of Kingston, New York. *Anabaena cylindrica* was obtained from laboratory cultures. Plant materials were frozen, lyophilized, and ground (0.4 mm, using a Wiley mill).

Laboratory microcosms

Twenty-four cylindrical polypropylene microcosms (6.5 cm diameter × 11 cm depth) were filled with 100 g wet weight of experimental sediment. Then, microcosms were randomly selected to receive one of four plant material treatments (100 mg of *V. americana*, *A. rubrum*, *A. anabaena* or no addition of plant material) and one of two amphipod treatments (2 or 0 individuals per container). Thus, there were 3 replicates for each of the 8 possible combinations. Each of the 24 microcosms was filled with Hudson River water and placed randomly in a holding tray where the water was filled to a level just below the top of all the microcosms. Water from this region of the Husdon is generally high in nutrients; nitrate and total dissolved phosphate average near 50 uM and 1 uM, respectively (Cole et al., unpublished). We chose to keep the water in each microcosm isolated from others because of the potential for pigment contamination and also to prevent amphipod escape. Water in each of the microcosms was exchanged with fresh river water once a week for the first month and biweekly thereafter. The nitrogen supplied would allow for a doubling of percent nitrogen, but the 50:1 N:P ration in water may result in phosphorus limitation. The holding tray was kept in the dark in an environmental chamber at 15 °C for the duration of the experiment (77 days). Two small sediment cores (4 mm inner diameter) were taken from each microcosm for pigment analysis at 1, 14, 42 and 77 days after addition of plant material. Dead amphipods were replaced with amphipods of similar size throughout the experiment.

Pigment analyses

Pigments were extracted from sediments using 100% acetone to reduce artifactual production of chlorophyllide (Jeffrey & Hallegraeff 1987). Pigment extracts were sonicated for 5 min. and allowed to stand overnight in the dark at 4 °C, prior to centrifugation at 3000 rmp for 3 min. in 15 ml polypropylene centrifuge tubes. The tubes were capped and stored frozen prior to pigment analysis. Pigments were determined by ion-pairing, reverse-phase HPLC (Mantoura & Llewellyn 1983). The ion-pairing (1.5 g tetrabutylammonium acetate and 7.7 g of ammonium acetate, made up to 100 ml with water) allows for greater resolution of the dephytolated acidic chloropigments (chlorophyll *c*, chlorophyllide *a*) (Mantoura & Llewellyn 1983).

The equipment employed consisted of a gradient pumping system (Varian-Vista 5500) controlled by a Vista 402 dual-channel system. Dual-channel detection was achieved with a Varian-Vista UV monitor set at 440 nm for absorbance and a Kratos Spectroflow 980 fluorescence detector, with an excitation at 440 nm and emission at 700 nm. An auto-injector equipped with a Rheodyne model 7126 valve was connected via a precolumn to a reverse-phase C_{18} Adsorbosphere column (5 μm particle size; 250 mm × 4.6 mm i.d). After injection (100 μl sample), a gradient program that ramped (1 ml/min.) from 100% mobile-phase A (80:10:10 ml, methanol: water; ior-pairing reagent) to 100% mobile-phase B (70:30 ml, methanol; acetone) in 30 min. with a hold for 20 min. provided sufficient resolution for all pigments of interest except for β-carotene and phaeophytin *a* (Fig. 1). The column was re-equilibrated between samples by linear ramping to a 100% mobile-phase A for 4 min.

Identification of all pigments was confirmed by comparing absorption spectra obtained with a Waters 990 photo diode-array detector with that of published values (Davies 1976; Braumann & Grimme 1981; Mantoura & Llewellyn 1983; Wright & Jeffrey 1987). Calibration standards for chlorophylls *a* and *b* were obtained from Sigma Chemical Co. Identification standards for carotenoids (lutein and fucoxanthin) were obtained from Rodger Dawson at the University of Maryland, Chesapeake Biological Laboratory, through his participation in an NSF-sponsored pigment calibration program, GOFS, organized by R.R. Bidigare and M.C. Kennicutt II at Texas A & M University. Retention time was also used as a parameter for identification based on the inter-calibration measurements obtained from the pigment calibration program. Concentrations of pigment standards were determined spectrophotometrically (Perkin-Elmer 552), in 1 cm cuvettes, using published extinction coefficients (Mantoura & Llewellyn 1983). Known quantities of different pigments were injected and the

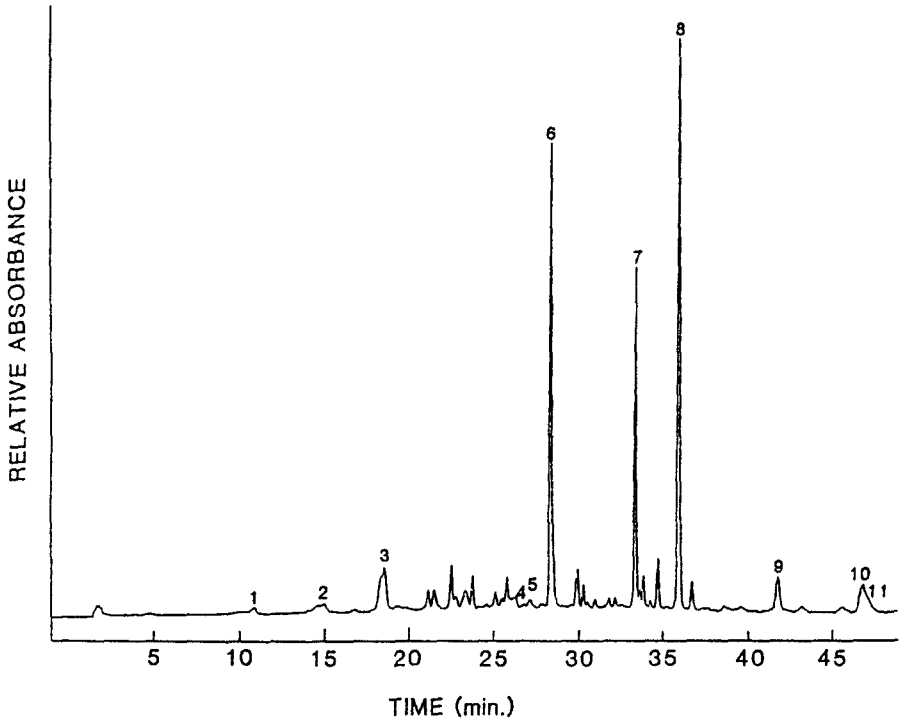

Fig. 1. Absorbance chromatogram of pigments in *Vallisneria americana* treatment with amphipods (on day 14), analyzed by ion-pairing reversed-phase HPLC. Peaks are numered as follows: (1) chlorophyllide *a*, (2) chlorophyll *c*, (3) phaeophorbide, (4) lutein 5,6 epoxide, (5) antheraxanthin, (6) lutein, (7) chlorophyll *b*, (8) chlorophyll *a*, (9) phaeophytin *b*, (10) β-carotene, (11) phaeophytin *a*.

determined peak areas were used to calculate response factors. Pigment concentrations of sediment extracts corrected for sample dilution and extraction efficiency, were then calculated with these response factors. We calculated β-carotene and phaeophytin *a* concentrations using peak area differences between absorbance and fluorescence chromatograms.

Chlorophyll *a* and *b* derivatives were produced from chlorophyll extracts (Sigma Chem. Co.), dissolved in 100% acetone, *Anacystis nidulans* (chlorophyll *a*) and spinach (chlorophyll *b*). Phaeophytins *a* and *b* were produced by acidification (30 μl of 2 N HCL added to 1 ml of pigment solution) followed by a clean-up separation using Chromprep cartridges (Hamiliton) to remove the acid. Chlorophyllide *a* was prepared by activation of chlorophyllase in the diatom cultures (*Thalassiosira* sp.) by overnight incubation in the dark with 50% aqueous acetone. Phaeophorbide *a* was prepared by acidification (30 μl of 2 N HCL added to 1 ml pigment solution) of the chlorophyllide from the above preparation.

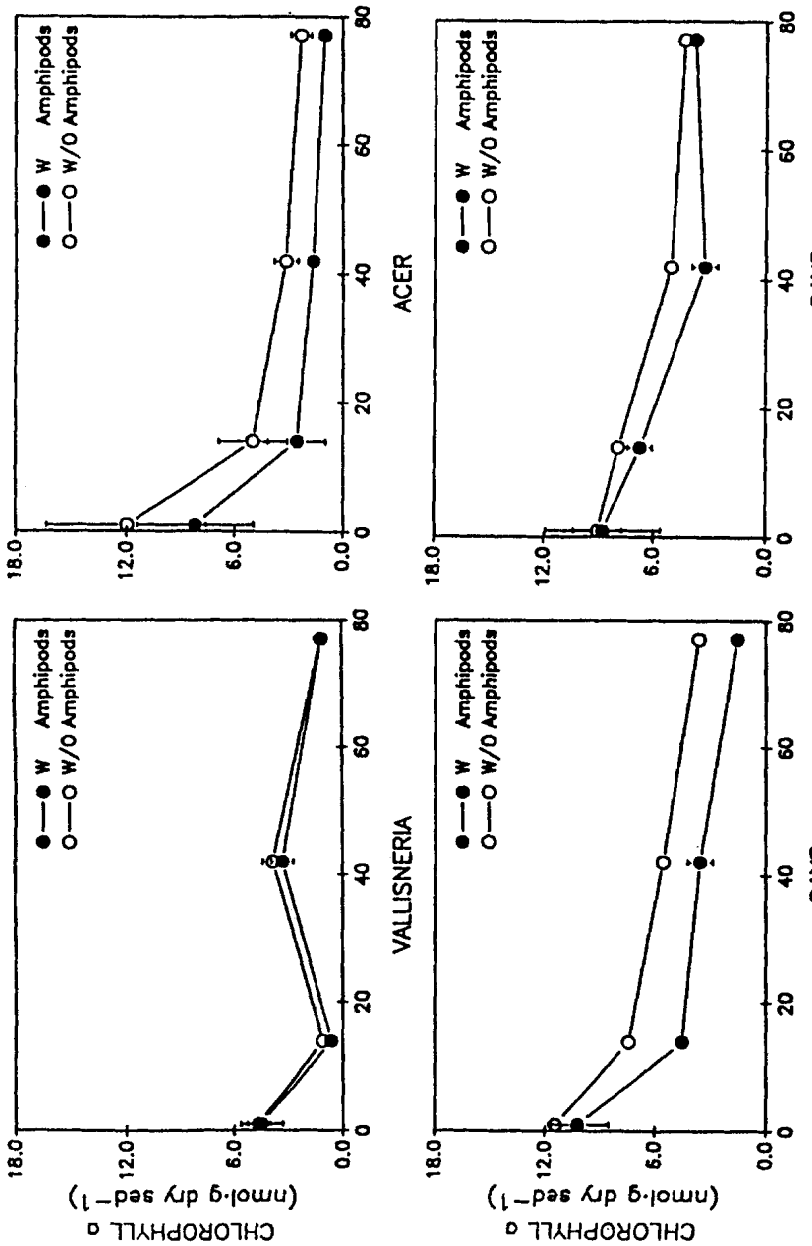

Fig. 2. Concentrations of chlorophyll *a* (nmol g dry sed-1) in sediments from microcosms containing different detrital sources with and without amphipods.

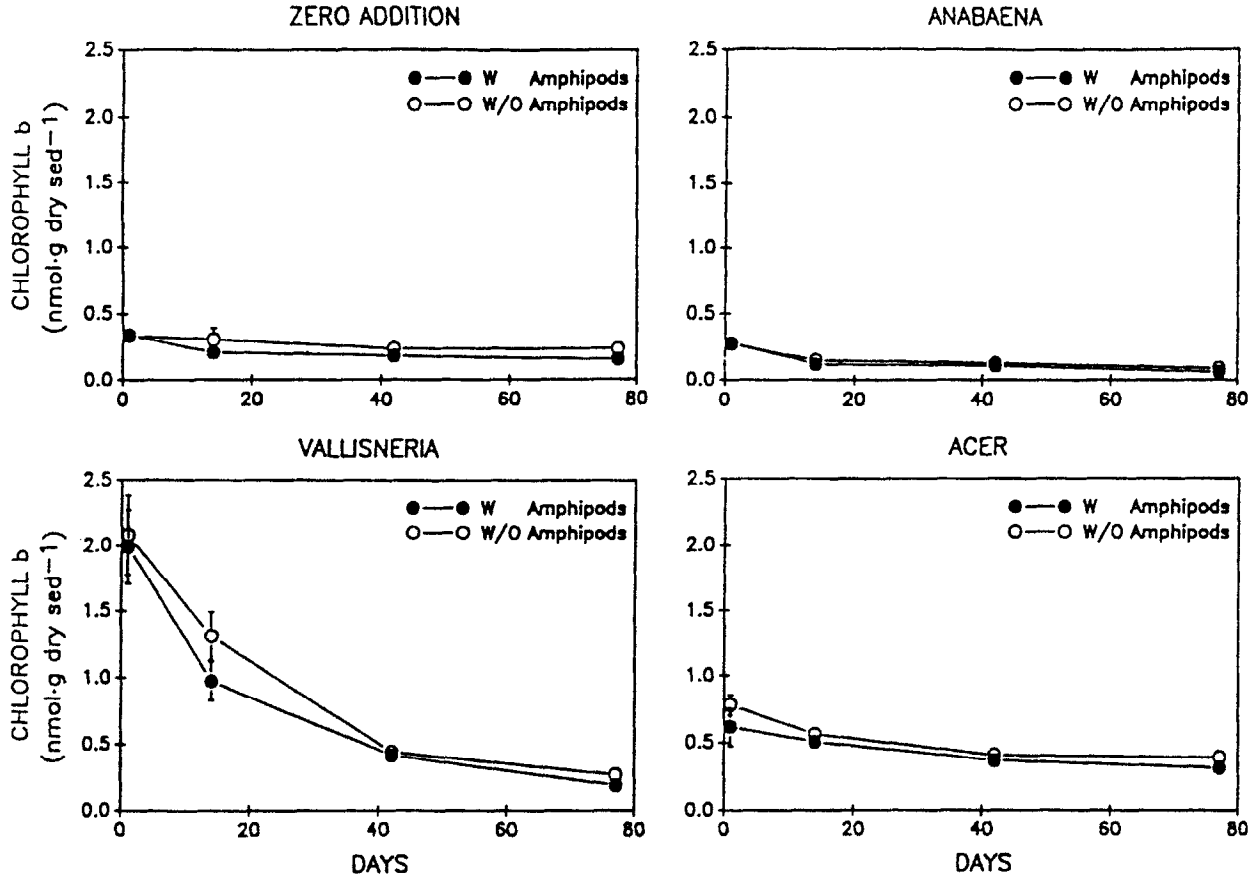

Fig. 3. Concentrations of chlorophyll *b* (nmol g dry sed-1) in sediments from microcosms containing different detrital sources with and without amphipods.

Although a number of phaeophorbide *a*-like components have been reported in the literature (Mantoura & Llewellyn 1983; Hawkins et al. 1986; Riaux-Gobin et al. 1987), phaeophorbide *a* produced by this procedure appears as a single dominant peak.

These data were used in a repeated measures three-way ANOVA with replication (Gurevitch & Chester 1986), with plant type, time interval, and amphipods as the main effects. A repeated measures test was used because the sequential samples collected from the microcosms are not independent. We calculated the difference in concentration between each pair of the sampling points divided by time, to generate a set of observations of rates of changes in pigment concentration for three time intervals for each microcosm. This approach allows to detect statistical differences in pigment dynamics with plant type and amphipods as main effects. The Scheffe'multiple range test was used to test for differences among treatments (Sokal & Rohlf 1981).

Results

All plant material additions resulted in significant rates of increase in concentrations of chloropigments relative to the zero-addition control, except for chlorophyll *b* after the addition of *A. cylindrica* — which does not contain chlorophyll *b* (Figs 2 and 3). Contrary to the pigment results, there was no detectable increase in sediment organic matter after addition of plant material (data not shown). Differences in decay rates of pigments were made at varying time intervals over the 77 day experimental period.

Chloropigment transformation

Chlorophylls *a* and *b* decreased significantly (ANOVA $P < 0.001$) over time in all plant treatments (Figs 2 and 3). The rate of decrease in chlorophyll *a* concentrations over time was significantly faster ($P < 0.05$) in *A. cylindrica* than in the *V. americana* and *A. rubrum* treatments. Concentrations of chlorophyll *a* decreased significantly ($P < 0.05$) faster in the *V. americana* treatment with amphipods. For the two plant types that contain chlorophyll *b* (*V. americana* and *A. rubrum*), concentrations of chlorophyll *b* also decreased significantly faster ($P < 0.05$) in *V. americana.*

Rates of increase of phaeopigments, phaeophorbide and phaeophytin, were significant (ANOVA, $P < 0.001$) over time for all plant treatments with the exception of phaeophytin *b* in the *A. cylindrica* treatment

(Figs 4—6). Rates of increase of phaeophytin *a* concentrations were not significantly different ($P > 0.05$) among any of the four plant treatments nor were there any significant amphipod effects. For the two plant types containing chlorophyll *b*, the rates of increase in phaeophytin *b* concentrations were not significantly different ($P < 0.05$) between *V. americana* and *A. rubrum*. The presence of amphipods had no significant ($P > 0.05$) effects on rates of increase in phaeophytin *b* concentrations for these two treatments. Rates of increase in total phaeophorbide concentrations were significantly higher ($P < 0.05$) in *V. americana* and *A. cylindrica* treatments than in the *A. rubrum* and the zero addition treatments. Rates of increase in phaeophorbide concentrations were significantly higher ($P < 0.05$) in the presence of amphipods for the *V. americana* and *A. cylindrica* treatments.

Carotenoid transformation

Rate of decrease for lutein concentrations decreased significantly (ANOVA, $P < 0.05$) over time for all plant treatments (Fig. 7). Amphipods and plant type had no significant effect ($P > 0.05$) on the rate of lutein loss.

Discussion

This experimental study points to the utility of plant pigments as tracers of inputs of plant material in aquatic ecosystems. The total input in these experiments was 15 g C/m^2 applied as a single dose. Such a rate of input is equivalent to roughly one to three weeks of carbon sedimentation in eutrophic lakes or nearshore waters (Bloesch et al. 1977; Zeitzschel 1980). This input resulted in a detectable change in sedimentary pigment concentrations and composition, with these changes persisting for at least one month.

Heterotrophic transformation of pigments

The heterotrophic transformation of chlorophylls *a* and *b* was faster in resources of greater nitrogen content which were presumably of higher quality to heterotrophs (Tenore et al. 1982; Webster & Benfield 1986). Rate of loss of chlorophyll *a* in the first 14 days was fastest in *A. cylindrica* followed by *V. americana* and *A. rubrum* (Fig. 2). Similarly,

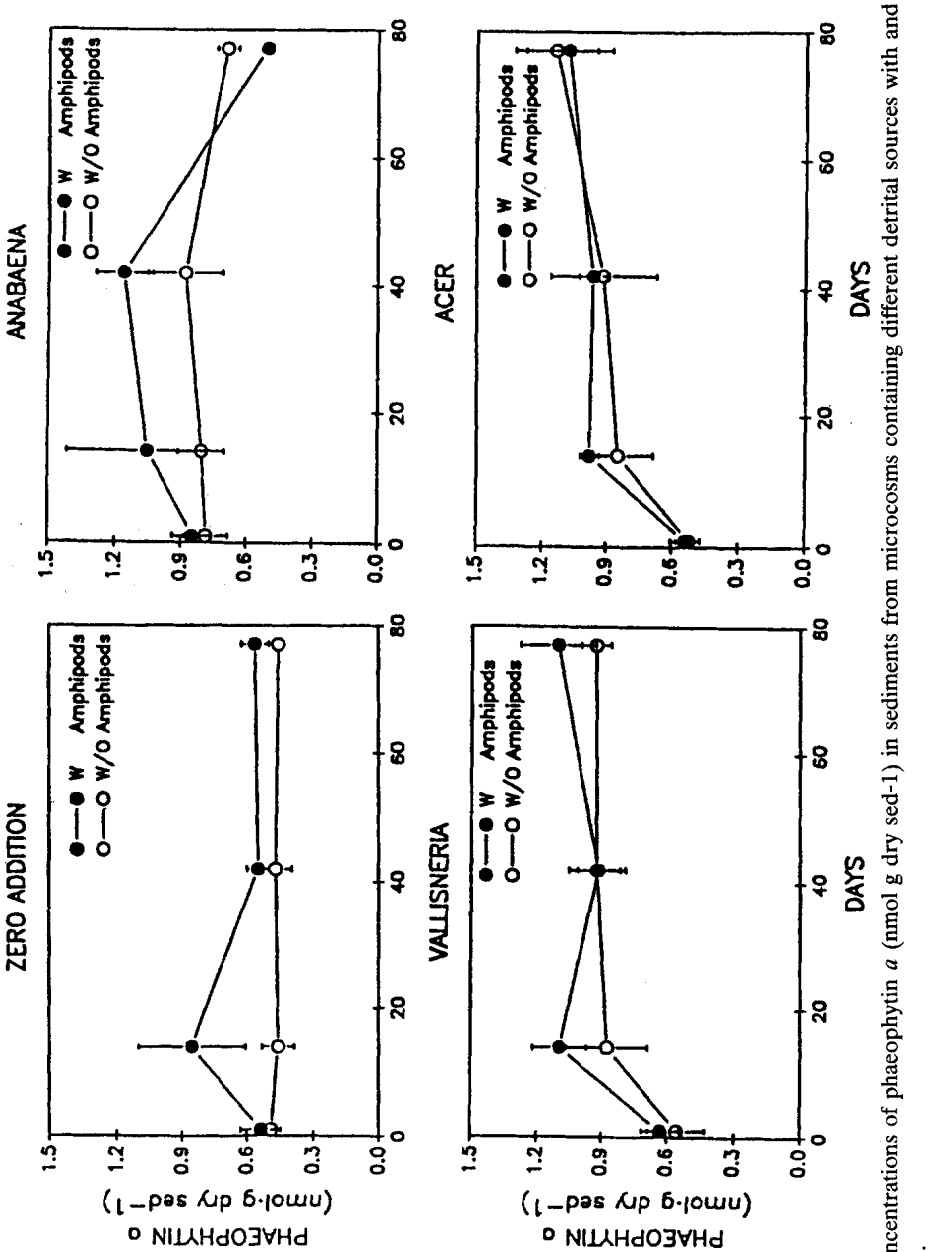

Fig. 4. Concentrations of phaeophytin *a* (nmol g dry sed-1) in sediments from microcosms containing different detrital sources with and without amphipods.

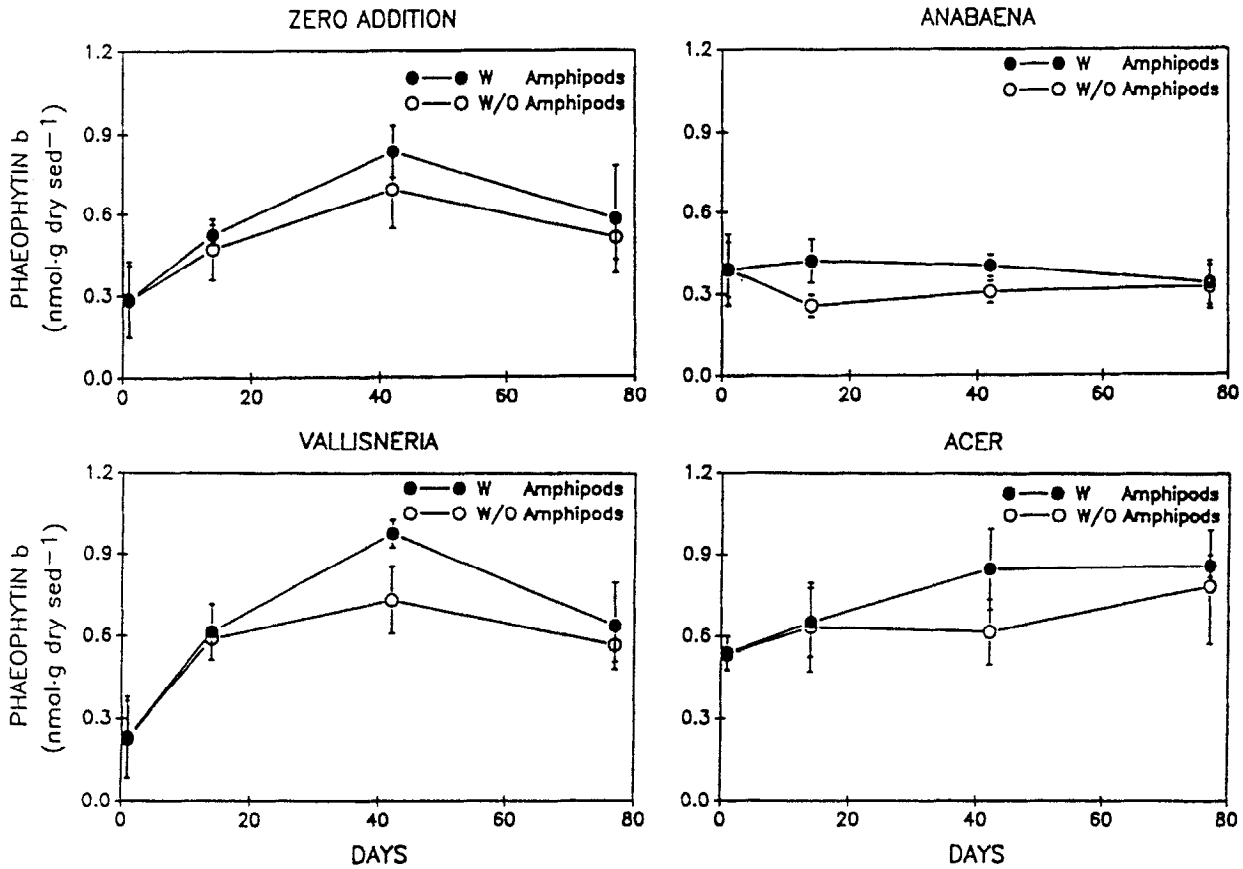

Fig. 5. Concentrations of phaeophytin *b* (nmol g dry sed-1) in sediments from microcosms containing different detrital sources with and without amphipods.

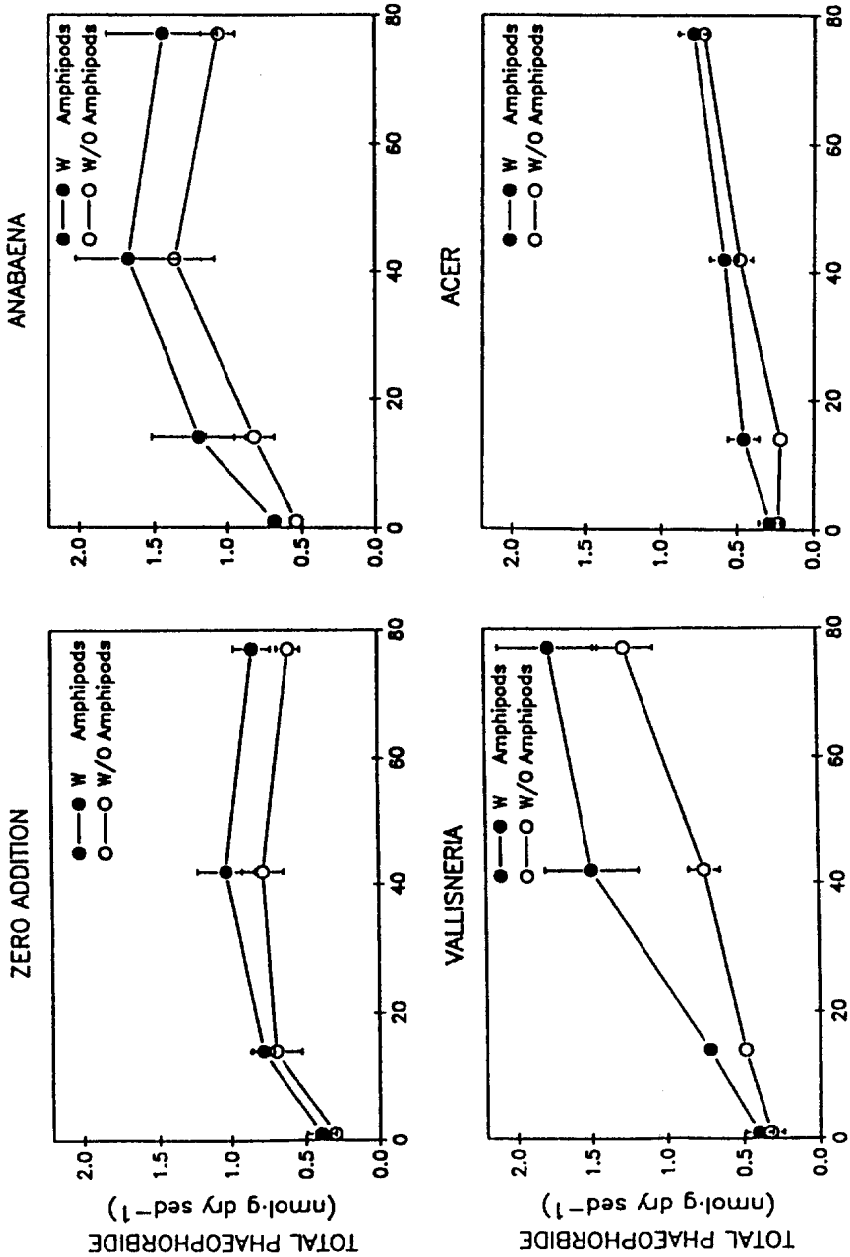

Fig. 6. Concentrations of total phaeophorbide (nmol g dry sed-1) in sediments from microcosms containing different detrital sources with and without amphipods.

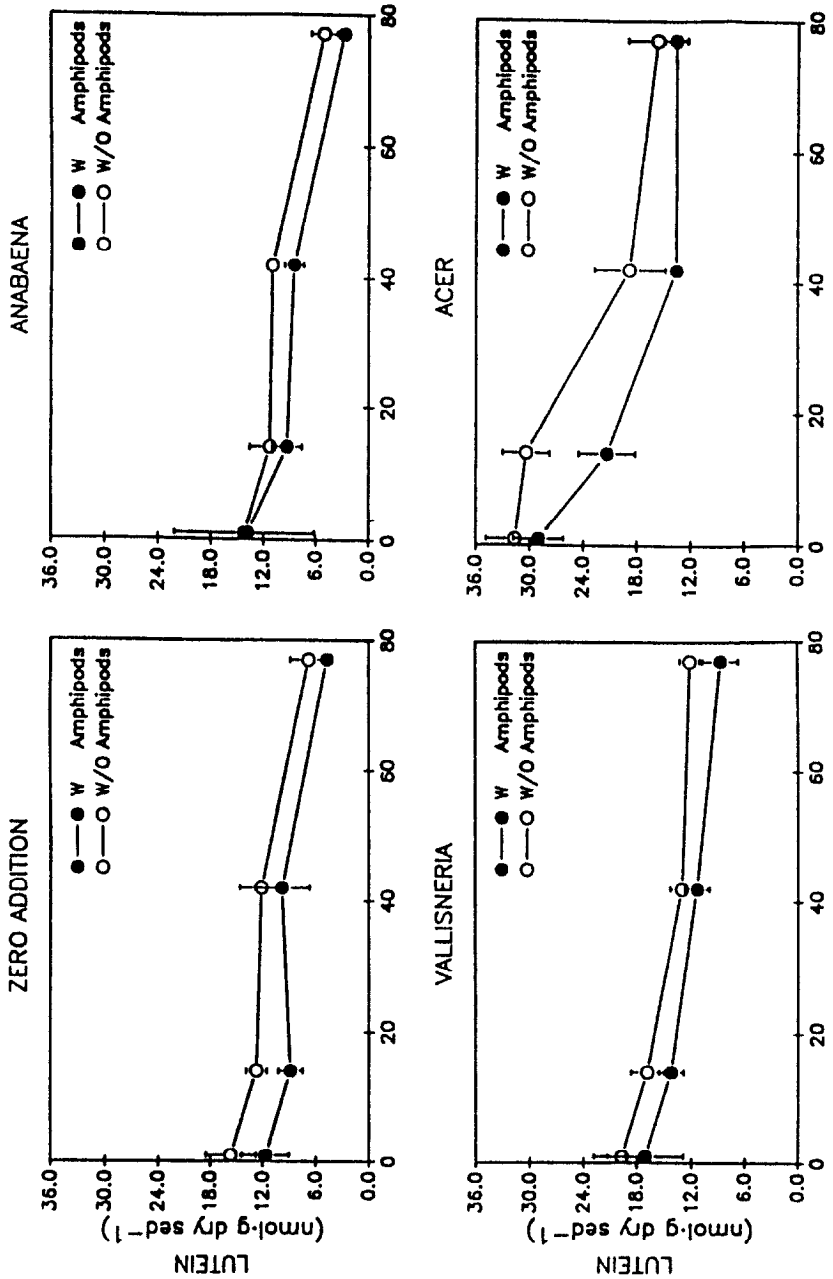

Fig. 7. Concentrations of lutein (nmol g dry sed-1) in sediments from microcosms containing different detrital sources with and without amphipods.

chlorophyll *b* loss was faster in the *V. americana* treatment than in the *A. rubrum* treatment (Fig. 3). Some of the fundamental qualitative differences between these resource materials can be attributed to differences in the organic carbon:nitrogen (C/N) ratio (*A. cylindrica*, 5.02 ± 0.08 (±SE): *V. americana*, 11.49 ± 0.89; *A. rubrum*, 60.22 ± 1.14) and the concentration of structural compounds (i.e., lignin). Nitrogenous components of non-vascular plants are more likely to contribute to the nutrition of detritivorous consumers that vascular plants (Findlay & Tenore 1982). Vascular plants contain more ligneous and phenolic compounds, which can also reduce resource availability to consumers (Valiela et al. 1979; Rice & Tenore 1981; Harrison 1982).

The lack of macrofaunal (amphipods) effects on the conversion of chlorophylls *a* and *b* to phaeophytin on different source materials suggests that this degradative pathway may be primarily controlled by the microbial community (Fig. 4). In a previous study, Bianchi et al. (1988) reported similar results on degradative pathways of chloropigments in sediments that also supported a microbial mechanism for the production of phaeophytin. However, other studies have demonstrated that grazing by certain protozoans can also produce phaephytin (Klein et al. 1986).

Production of total phaeophorbides was generally higher in treatments with amphipods grazing on high quality plant resources. This agrees with other studies that show chlorophyll is converted to phaeophorbide by metazoan grazing (Shuman & Lorenzen 1975; Bricelj 1984; Carpenter & Bergquist 1985; Hawkins et al. 1986; Bianchi et al. 1988). Total (integrated) phaeophorbide production in plant material addition treatments was estimated by integrating areas under the curves, then subtracting phaeophorbide production observed in the zero-addition treatment. Phaeophorbide production in the *A. cylindrica* treatment with amphipods was 12% more than the *V. americana* and 58% greater than the *A. rubrum* plant treatments (Fig. 6). After only 14 days, consumers feeding on the high quality resource *A. cylindrica* had already produced 25% of the total phaeophorbide production as compared with 15% in the *V. americana* treatment. As might be expected, more phaeophorbide production in high quality resources occurs earlier than in more recalcitrant sources. Phaeophorbides represent approximately 40—45% of the total phaeopigment pool in *A. cylindrica* and *V. americana* treatments with amphipods, compared with 25% in the *A. rubrum* treatment. The total phaeopigment pool in this case includes phaeophytins *a* and *b* and total phaeophorbides; chlorophyllides, primed and allomeric compounds were not included. Any increases in the production of phaeopigments in the zero treatment can probably be explained by microheterotrophic activity on sedimentary organic matter.

The loss of the carotenoid, lutein, was not different among different plant types (Fig. 7). Lutein is believed to be converted to lutein epoxide by certain bacteria (Repeta 1989). Lutein is considered to be one of the more decay-resistant carotenoids when compared to fucoxanthin, peridinin, and diadinoxanthin, because the parent molecule lacks the 5, 6 epoxide that is present in the other carotenoids (Repeta & Gagosian 1987). Previous results suggest that changes in lutein concentrations, based on calculated first-order decay rates, should be slower in the more recalcitrant plant sources (Bianchi & Findlay 1991). In this experiment, all materials were ground to the same size and then introduced to the sediments, unlike the previous work which looked at pigment decay in whole plants.

Compositional differences in the production of particular phaeopigments can provide useful information for investigating the trophic dynamics of natural systems. For example, in this study we have demonstrated that total phaeophorbide is positively correlated with macrofaunal grazing activity. We also know that the amount of chlorophyll converted to phaeopigments is strongly affected by the quality of the resource. Production of phaeophytin does not seem to be as dependent on macrofaunal activity or qualitative differences in the source material. This type of "ground-truthing" information can be useful for interpreting the effects of temporal and spatial variability of different resource inputs to the trophic dynamics of aquatic systems. In particular, these laboratory results corroborate the relationship that we find between phaeophorbide concentrations grazing activity and food resource quality in the Hudson River food web (Bianchi & Findlay 1991). Further "ground-truthing" information from different systems, obtained through laboratory experimentation, will continue to provide the necessary pigment bio-markers needed for studying natural ecosystems.

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